"Mathematical Contributions to the Theory of Evolution. VI. Reproductive or Genetic Selection. Part I. Theoretical." By KARL PEARSON, F.R.S. "Part II. On the Inheritance of Fertility in Man." By KARL PEARSON, F.R.S., and ALICE LEE. "Part III. On the Inheritance of Fecundity in Thoroughbred Race-horses." By KARL PEARSON, F.R.S., with the assistance of LESLIE BRAMLEY-MOORE. Received November 14—Read December 8, 1898.

(Abstract.)

1. The object of this memoir is twofold: first, to develop the theory of reproductive or genetic selection* on the assumption that fertility and fecundity may be heritable characters; and, secondly, to demonstrate from two concrete examples that fertility and fecundity actually are inherited.

The problem of whether fertility is or is not inherited is one of very far reaching consequences. It stands on an entirely different footing to the question of inheritance of other characters. That any other organ or character is inherited, provided that inheritance is not stronger for one value of the organ or character than another, is perfectly consistent with the organic stability of a community of individuals. That fertility should be inherited is not consistent with the stability of such a community, unless there be a differential death-rate, more intense for the offspring of the more fertile, *i.e.*, unless natural selection or other factor of evolution holds reproductive selection in check. The inheritance of fertility and the correlation of fertility with other characters are principles momentous in their results for our conceptions of evolution; they mark a continual tendency in a race to progress in a definite direction, unless equilibrium be maintained by any other equipollent factors, exhibited in the form of a differential death-rate on the most fertile. Such a differential death-rate probably exists in wild life, at any rate until the environment changes and the equilibrium between natural and reproductive selection is upset. How far it exists in civilized communities of mankind is another and more difficult problem, which I have partially dealt with elsewhere.† At any rate it becomes necessary for the biologist either to affirm or deny the two principles stated above. If

* I have retained the term "reproductive" selection here, although objection has been raised to it, because it has been used in the earlier memoirs of this series. Mr. Galton has kindly provided me with "genetic" and "proliferal" selection. The term is used to describe the selection of predominant types owing to the different grades of reproductivity being inherited, and without the influence of a differential death-rate.

† Essay on Reproductive Selection in 'The Chances of Death and other Studies in Evolution,' vol. 1, p. 63.

he affirms them, then he must look upon all races as tending to progress in definite directions—not necessarily one, but possibly several different directions, according to the characters with which fertility may be correlated—the moment natural selection is suspended; the organism carries in itself, in virtue of the laws of inheritance and the correlation of its characters, a tendency to progressive change. If, on the other hand, the biologist denies these principles, then he must be prepared to meet the weight of evidence in favour of the inheritance of fertility and fecundity contained in Parts II and III of the present memoir.

2. The theory discussed in Part I opens with the proof that if fertility be a function of any physical characters which are themselves inherited according to the law of ancestral heredity, then it must itself be inherited according to that law. As fertility would certainly appear to be associated with physique, we have thus an *à priori* argument in favour of its inheritance.

3. In the next place the influence of "record" making on apparent fertility is considered. The mother with more offspring has a greater chance than one with fewer of getting into the record which extends over several generations, and, further, if every possible entry be taken from the record, she is again weighted with her fertility. Thus a record is not a true account of the fertility of successive generations. The fertility of mothers is always found to be more and their variability less than the fertility and variability of daughters. Accordingly from the apparent fertility and variability of the record the actual values in each generation must be deduced. The difficulties and the theory of this investigation are developed at some length, and methods determined by which it can be ascertained whether a secular change in fertility is actually taking place. The results obtained are extended to fecundity.

4. In the case of thoroughbred horses, their number is so few and in-breeding so great owing to the fashion in sires and stocks, that we have to deal with a large array of offspring of the same sire. It is easy accordingly to obtain 50,000 to 150,000 pairs of a given relationship, *e.g.*, half-sisters, and we rapidly get numbers too large for forming correlation tables in the usual manner. Accordingly methods are developed for finding correlation coefficients from the means of "arrays." These methods are of considerable importance, for they enable us to ascertain the correlation between a latent character in one sex and a patent character in another, or between characters latent in two individuals. Thus, it is shown that the correlation between the brood-mare's fecundity latent in two related stallions can be deduced from the correlation between the mean fecundities of their two arrays of daughters. In this way a numerical estimate can be formed of the inheritance of latent characters.

5. The brood-mare is for many causes, detailed at length in the paper, a highly artificial product, and accordingly the record gives a considerable percentage of fictitious fecundities. The effect of a mixture of correlated and uncorrelated material on correlation and variation is next investigated, and it is shown that the former is more seriously affected than the latter. Hence results based on variation are more likely to be trustworthy than those which use correlation. Incidently the problem of the mixture of heterogeneous materials uncorrelated in themselves is investigated, and it is shown that a correlation will result in the mixture. This *spurious* correlation is of some importance for the question of mixtures of classes in fertility problems, but it is also significant of the general danger of heterogeneity in bio-statistical investigations, and further indicative of the possibility of creating correlation between two characters by breeding between small heterogeneous groups in which this correlation is zero. This illustration suffices to indicate how correlation between characters does not necessarily indicate a causal relationship.

6. Part II of the memoir deals with the inheritance of fertility in man. It is first shown by large numbers that fertility is undoubtedly inherited from mother to daughter, but that if we include all types of marriages the inheritance is largely screened by other factors. An attempt is made to remove one by one these factors, and the more stringently this is done the more nearly the regression of daughter on mother moves up towards the value required by the law of ancestral heredity. If we could take only marriages in which both daughter and mother were married during the whole of their fecund period there is little doubt that we should find inheritance according to the law of ancestral heredity. The sparseness of homogeneous material hinders, however, such an investigation.

The inheritance of fertility from father to son is then considered; this is really rather an inheritance of sterility or tendency to sterility, for the full fecundity of a man is not usually exhibited in monogamic union. It is rather a problem of whether his fecundity lasts as long as his wife's. We find definite inheritance of this sterile tendency from father to son, although for the reason just given it falls below that indicated by the law of ancestral heredity.

Lastly, the inheritance of fertility in the woman through the male line is dealt with, and it is shown that a woman's fertility is as highly correlated with that of her paternal as with that of her maternal grandmother. In other words the latent character, fertility in the woman, is transmitted through the male line, and with an intensity which approximates to that required by the law of ancestral heredity. Incidentally the problem of "heiresses" is dealt with. It is shown that in the case of women who are chiefly "heiresses," there is at once a considerable drop in the correlation between their fertility and that of

their mothers, while there is a small drop only in their average fertility. In other words, an "heiress" is not to be looked upon as coming in general from a sterile stock, but as having a mother, whose fertility has a fictitious value, *i.e.*, the apparent fertility of the record is not the potential fertility, the inherited character, in the mother. In other words "heiresses" are not as a rule due to sterile mothers, but in the bulk are due to such causes as late marriages, restraint, incompatibility of husband and wife, absence of sons or death of other children, &c., &c.

7. Part III of the memoir contains the results of a somewhat laborious investigation into the fecundity of brood-mares, which has been a number of years in progress. Had better material been available for the inheritance of fecundity, we would gladly have adopted it in preference to dealing with such an intricate subject as the breeding of race-horses. Unfortunately the absence of place and means hindered any experimental investigation on our part into the inheritance of fecundity in some simpler type of life. Such investigation ought certainly to be made by a trained biologist with the knowledge and the laboratory at his disposal.

After discussing at length the steps taken by us to measure and tabulate the fecundity of brood-mares, we deduce the following conclusions :—

(i.) Fecundity in the brood-mare is inherited from dam to mare.
(ii.) It is also inherited from grand-dam to mare through the dam.

In both these cases the intensity is much less than would be indicated by the law of ancestral heredity, but the divergence is not such that it could not be accounted for by a percentage of fictitious values such as the peculiar conditions of horse-breeding warrant us in considering probable.

(iii.) The latent quality, fecundity in the brood-mare, is inherited through the sire; this is shown not only by the correlation between half-sisters, but by actual determination of the correlation between the latent character in the sire and the patent character in the daughter.
(iv.) The latent quality, fecundity in the brood-mare, is inherited by the stallion from his sire. This is shown not only by the fecundity correlation between a sire's daughters and his half sisters, but also by a direct determination of the correlation between the latent quality in the stallion and in his sire.

In both these cases of latent qualities the law of inheritance approaches much more closely to that required by the Galtonian rule This is probably due to the fact that the determination of the correlation is thrown back on the calculation of the means and variabilities of

arrays, and not on the direct calculation of the correlation between fecundities, a large percentage of which are probably fictitious (see § 5).

8. Parts II and III accordingly force us to the conclusion that fertility is inherited in man and fecundity in the horse, and therefore probably that both these characters are inherited in all types of life. It would indeed be difficult to explain by evolution the great variety of values these characters take in allied species, if this were not true. That they are inherited according to the Galtonian rule seems to us very probable but not demonstrated to certainty. It is a reasonable hypothesis until more data are forthcoming.

The memoir concludes with a discussion of the meaning of reproductive selection for the problem of evolution and with sixteen correlation tables, giving the dressed material on which our conclusions are based.

"'Nitragin' and the Nodules of Leguminous Plants." By MARIA DAWSON, B.Sc. (Lond. and Wales). Communicated by Professor H. MARSHALL WARD, F.R.S. Received November 19, —Read December 8, 1898.

(Abstract.)

A study of the nodules found upon the roots of leguminous plants has led the author to an unhesitating confirmation of the parasitic nature of both the filaments and the bacteroids contained in these organs. The filaments, it was found, have no such constant relation to the nucleus of the cells, as was represented by Beyerinck in 1888. By plasmolysis of the root-hairs, the infection tube is shown to have grown into the hair, and not to correspond with the primordial utricle of the hair, a result which proves that Frank was mistaken in regarding the tube as formed from the contents of the hair mingled with fungal protoplasm. By staining with aniline blue and orseillin these tubes and the filaments in the cells were shown to consist of strands of straight rodlets, lying parallel to the longer axis of the filament, and embedded in a colourless matrix. This matrix does not consist of cellulose, chitin, or any form of slime. The swellings upon the filaments occur at places where the rodlets have become heaped up, and at such places the filaments eventually burst, liberating the rodlets, whilst they themselves remain as pointed portions, directed towards each other in the cells. After liberation from the filaments, the rodlets become transformed into X, V, and Y-shaped bacteroids. This variety of shape does not occur when these organisms are cultivated outside the plant on a solid medium, but in liquid pea extract the change from straight rodlets to "bacteroids" occurs in a few days. By cultivating these organisms in drop cultures under constant observa-